Article VIII.—Acanthocephala from the Illinois River, with Descriptions of Species and a Synopsis of the Family Neoechinorhynchidae.*
By H. J. Van Cleave.

Introduction

There has been no published record of extensive study upon the Acanthocephala from fresh-water hosts for any part of North America. The only regional studies pursued in this country have been those of Linton (1889, 1891, 1901, and 1905) on the Acanthocephala of marine fishes, from New England southward along the Atlantic Coast. Most of the European studies aside from Zschokke's (1884), and a few others, have been compilations of host records from results of investigations in widely scattered regions. Usually these lists have ignored the geographical distribution of the parasites or have implied for them a distribution equivalent to the distribution of the hosts. Because of inaccuracies in many of the early investigations and the numerous erroneous identifications of European species these lists have comparatively little biological value.

The present paper is based upon an intensive search for Acanthocephala in the vertebrates of the Illinois River, especially in the region of Havana, Illinois. The collections were the result chiefly of work during the summer of 1910, though a number of subsequent observations have been included in the tabulated results along with a few instances of hosts examined at other points on the river, namely at Peoria and at Beardstown, Illinois.

It is especially significant that the first study of this sort should be upon forms found in the Illinois River. The life of this stream has received so much attention at the hands of Professor Forbes and his associates in the Illinois Natural History Survey that the studies relating to its life have frequently been referred to as the first significant and the most extensive of those dealing with river life. Hitherto practically no attention has been directed to the parasitic fauna of this region. The interrelationships existing between internal parasites and their hosts are of such fundamental nature that no survey of the life of any region is complete if the parasitic fauna is left out of consideration.

Acknowledgments

Generous cooperation on the part of a number of individuals has enabled me to present a more complete study of fresh-water represen-

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tatives of this group than has ever been possible heretofore. Professor H. B. Ward has placed his collections and records from Havana, Illinois, at my disposal. Mr. R. H. Linkins has permitted the publication of two specific definitions which have previously occurred only in manuscript, concerning which a fuller statement is given later in this paper. I am especially indebted to Dr. G. R. La Rue for numerous collections of specimens including representatives of two new species. Collections of the U. S. National Museum and of the Bureau of Animal Industry, received through the courtesy of Dr. C. W. Stiles and Dr. B. H. Ransom, with the private collections of Dr. A. S. Pearse and of Dr. A. R. Cooper, have furnished an abundance of material for comparative study.

HABITS OF THE ACANTHOCEPHALA

THE LIFE CYCLE

The present paper deals with one of the most highly specialized groups of animal parsites in its relations to its hosts. The Acanthocephala are a group of worms the individuals of which reach sexual maturity in the digestive tract of various vertebrates. Life histories are not known with certainty for any of the species found in fresh-water hosts of North America, but there is no evidence that they ever lead an independent existence even for the shortest periods of time. Their development has been studied in a number of European species. In all instances it has been found that the embryos produced by the females never lose their resistant confining membranes after they are set free from the body of the definitive host until these embryos are taken into the body of the primary host. The primary host is usually an arthropod. Embryos of the Acanthocephala are taken into the digestive tract of the arthropod along with food. Here they are liberated from their confining shells and undergo further development within the body of the primary host. Intermediate hosts are not infrequent in the life cycle of the Acanthocephala. If primary hosts bearing larval Acanthocephala are eaten by an animal in which the larvae are unable to complete their development, the larvae become encysted in the tissues of the new host. The entrance into the definitive host is, in this instance, contingent upon the intermediate host's serving as food for the definitive host. The parasite never reaches sexual maturity unless the primary or intermediate host is eaten by a vertebrate in which the worm is capable of continuing its development. Thus the parasite is in every step of its development dependent upon some other organism for its maintenance. This absolute dependence of the Acanthocephala makes a study of their interrelationships with the host a topic of considerable economic importance. This is true even though the host affected may not be of direct commercial value to man. The interdependence of life in the same habitat has been so frequently emphasized that it need not be discussed fully here. One example will serve as an illustration. The gizzard-shad (Dorosoma cepedianum) has practically no direct commercial value, yet it serves to such great extent as food for the

most valued of fishes that any factor influencing the life and health of this shad has a distinctly economic bearing.

RELATIONS TO THE HOST

The injury inflicted upon the host by an endoparasite such as the Acanthocephala assumes several distinct aspects. Of these, three are the most readily observed: (1) mechanical injury to the host caused by the parasite; (2) physiological injury to the host through interference with the normal functioning of organs; and (3) physiological injury due to toxins produced by the parasite. For the Acanthocephala the first two of these are the most obvious. They cling to the walls of the digestive tract of the host by means of sharp spines and hooks located chiefly on a special organ of attachment called the proboscis. These hooks, in their normal functioning, pierce the wall of the intestine of the host, frequently producing thereby lacerations which are discernible as inflamed areas even on the outer surface of the intestine. Hofer (1906:231) has called attention to the fact that with age these areas become calcified. This condition has not been observed by the present writer. In some instances—for example in members of the genus Pomphorhynchus—the intestine may be completely perforated, so that the proboscis comes to lie within the body-cavity of the host. Such perforation occasionally leads to active migration of the parasite into the body-cavity of the host.

Through lacerations and perforation of the intestinal mucosa diseaseproducing organisms find ready access to the tissues of the intestine, and through the body-cavity and the blood stream reach all organs of the body. Thus infection is facilitated by the presence of the Acanthocephala, while under normal conditions the unbroken lining of the digestive canal

would resist the entrance of the disease-producing organisms.

Since the Acanthocephala have no trace of a digestive system they appropriate from the host intestine all of the elaborated food materials utilized in their metabolism. The effect of this loss upon the host is contingent upon the number of parasites it harbors. The writer has frequently seen fishes that were in poor flesh yield execessive numbers of Acanthocephala. There is no specific symptom, however, which will permit diagnosis of the presence of Acanthocephala by external examination of the body. Frequently the digestive tract for a considerable part of its extent becomes packed with these worms. In such quantities they effectively clog the digestive system by mechanical obstruction, and at the same time utilize such quantities of elaborated food that the supply available for the host is distinctly limited. The extent of injury to the host through toxic substances produced by these parasites has not been studied directly from either the chemical or the physiological point of view.

EXTENT OF INFESTATIONS

In the present study it has seemed inadvisable to attempt any analysis of percentages of infestation with Acanthocephala, since in many

instances the number of individuals examined for these parasites is too small to yield reliable data in this direction. One noticeable feature of the extent of infestation in this region should not be passed without comment. This is the adaptability of certain species to various hosts. It has been found that while a given species of parasite occurs in large numbers in certain host species it has been found occasionally in small numbers, frequently singly, in the intestine of different host species. This observation is especially true for the distribution of Echinorhynchus thecatus Linton. In a number of instances a single individual of this species has been found as a result of the examination of a fairly large number of fish of the same species, while practically every bluegill revealed a relatively large number of these worms. There are but few evidences of a fixed specificity of hosts such as are found in other parasite groups. In most instances differences in frequency of occurrence of these parasites are to be sought in differences in food habits of the hosts. Since the definitive host secures its Acanthocephala only through feeding upon the infested primary or intermediate host, the degree of infestation of the definitive host must be in some way correlated with the extent to which it preys upon the hosts of the larval parasite.

Influence of Age of Host on Infestation

Difference in degree of infestation within the same host species is frequently influenced by the age of the specimens of the host examined. The writer has frequently observed that young and very small fish may be free from acanthocephalan infestation even though the larger and presumably older specimens of the same species regularly carry parasites, The explanation of this difference has usually been sought in change of food habits by the fish at different ages. In the specimens of the gizzardshad examined by the writer the negative records are due in many instances to periodicity in the occurrence of the species of Acanthocephala infesting this fish (Van Cleave, 1916), but it has also been observed that small individuals of this species rarely reveal an infestation. In the light of the food habits of the gizzard-shad the reverse might well be expected. The food of the young of this species, according to observations by Forbes and Richardson (1908:47), consists "almost wholly of small crustaceans and insect larvae" while that of larger specimens comprises "quantities of mud, with which the intestine is commonly packed from end to end, mixed with many minute plants, and much vegetable debris." The present writer has also observed that macroscopic animal forms are but rarely represented in the stomach contents of larger specimens. In spite of the fact that the young of this species feed almost exclusively on small arthropods which might serve as primary hosts of Acanthocephala, they are rarely infested, while the larger specimens, which are to a great extent vegetable and detritus feeders, usually yield large numbers of Acanthocephala.

VERTEBRATES EXAMINED

The present study is limited to the parasites of three of the major groups of the Vertebrata; namely, Pisces, Amphibia, and Reptillia. No records of Acanthocephala from water-birds of the locality under consideration are available. It should be kept in mind, however, that most of our water-birds are migratory, and that consequently their parasitic fauna is not necessarily as characteristic of any restricted area as is the fauna parasitizing other fresh-water vertebrates. The writer (1918) has published the results of studies upon the Acanthocephala of birds from various parts of the United States. Little is known of the actual geographical distribution and restriction of the Acanthocephala parasitic in birds, and it is consequently unsafe to infer the presence of any given species of Acanthocephala in the Illinois River merely because it has been recorded from a species of bird whose range may include this locality. Inferences of this type have been common in the literature on parasitology, and they are responsible for many incorrect statements regarding the distribution of the parasitic fauna.

Table I
Assembled Data for all Species Examined
PISCES *

	Spp. of Acanthocephala found		Echinorhynchus thecatus	E. thecatus	E. thecatus Tangorhamphus longirostris Gravilisentis argailisentis		Pomphorhynchus bulbocolli Echinorhynchus thecatus	P. bulbocolts E. thecatus P. bulbocollis	Neoechinorhynchus cylindratus Octospinifer macilentus	Ecumornynchus thecutus Pomphorhynchus bulbocolli	Echinorhynchus thecatus P. bulbocolli P. bulbocolli	Echinorhynchus thecatus	Pomphorhynchus bulbocolli Echinorhynchus thecatus	Fompuornyments buttocom E. thecetus E. thecetus E. thecetus E. thecetus E. thecetus	Neoechimorhynchus cyfindratus B. thecatus E. thecatus
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	Ex- amined	1	16	ro	212	ø	20 20	16		-	63 69 63	9	11	616160	HOZH
PISCES *	Common names	Paddle-fish	Short-nosed gar	Fresh-water dogfish	nter Isospondyn Hodon tergisist LeS. Toothed herring Dorosoma cepedianum (LeS.)‡. Gizzard-shad	American eel	Mongrel buffalo Small-mouth buffalo	Common river carp		European carp	Channel-cat Speckled bullhead Black bullhead	White crappie	Black crappie	Rock bass Bluegill Pumpkinsed Small-mouthed black bass	Large-mouthed black bass Yellow perch Sheepshead
	Scientific names	Order Selachostomi Polyodon spathula (Walb.) †	omus (Raf.)	Order Cycloganolidea Amid calva Linn.	Hiodon tergisus LeS. Dorosoma cepedianum (LeS.) ‡	Order Apodes Anguilla chrysypa Raf.	Ictiobus urus (Agassiz)	Carpiodes carpio (Raf.)	Carpiodes velifer (Raf.)	Order Nematoenathi	Ameiurus mehus (LeS.). Ameiurus mehusus (LeS.).	Pomoxis annularis Raf	Pomoxis sparoides (Lacép.)	Amblophites rupestris (Raf.). Lepomts pallidus (Mitch.). Eupomotis gibbosus (Linn.). Micropterus dolomien Lacép.	M. salmoides (Lacép.)

		20 Neoechinorhynchus emydis	N. emydis		
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KEPTILIA§	Order Squamata Order contributor Linn. Order back snake	Pseudemys eleguns (Wied.) Slider	Graptemys pseudogeographica (Gray) Map turtle	Chelydra serpentina (Linn.)Common Snapper	Amyda spinifera (LeS.)Leather-back turtle

Rana pipiens Schreber Leapard frog
Rana catesbeitana Shaw Bullfrog
Bufo anergeans Bibly. AMPHIBIA § Order Salientia

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* In classification of Pisces that of Forbes and Richardson (1998) has been used
† The single specimen of Polyodon was taken at Beardstown, III., in August, 1912.
† Examinations of Dorosoma extended over a period of soveral years, including all seasons of the year and several
* records of acanthocopyinals infrestion from the Illinois at Peords.
§ Steinger and Barbour (1917) have been followed in the classification for Reptilia and Amphibia.

Adaptability to Different Host Species

A number of interesting facts regarding specificity of hosts in freshwater Acanthocephala may be observed in Table I. Tanaorhamphus longirostris, Gracilisentis gracilisentis, and Octospinifer macilentus are the only species recorded from a single host species. These all belong to the Neoechinorhynchidae. Their confinement to a single species is in sharp contrast to the adaptability displayed by Echinorhynchus thecatus and Pomphorhynchus bulbocolli. However, as O. macilentus is known to occur in a different species of sucker in another locality, the two species from the gizzard-shad are the only ones found in the locality under consideration which present strong evidence of restriction to a single host-species.

Members of the genus Echinorhynchus are among the commonest fish parasites, yet in the local fauna under consideration but a single species, *E. thecatus*, represents this genus. The relationship of this species to the host is obviously very generalized since it may find lodging in the bodies of fishes occupying widely different systematic positions. This species occurs not only in the more primitive orders of fish, but infests also representatives of practically every order of fish studied.

It is significant that for the region included in this survey no vertebrate host was found bearing larval Acanthocephala. Fish and amphibians frequently serve either as primary or intermediate hosts for encysted larvae which reach maturity in predaceous fish, birds, and mammals. Unfortunately, a number of species of snakes were examined before the writer began to keep negative records. The examination of snakes in other localities within the state, especially in the vicinity of Urbana, has without exception failed to reveal any Acanthocephala, either larval or adult.

In an earlier paper the writer (1915) has called attention to the infrequency of records of amphibian infestation by Acanthocephala in North America. Data in Table I are supplemented by his records of numerous examinations of both tailed and tailless Amphibia from other parts of the state, and none of these records shows acanthocephalan infestation for the amphibian fauna of the state.

Species newly credited to the Illinois River Fauna, and New Host-Records

The present study has added a number of new records concerning the distribution of Acanthocephala, the following four species being reported for the first time from Illinois: Echinorhynchus thecatus Linton (1891), Neoechinorhynchus cylindratus (Van Cleave, 1913), Pomphorhynchus bulbocolli Linkins, n. sp., and Octospinifer macilentus, n. sp.

For E. thecatus, twelve additional hosts are added; namely, Lepisosteus platostomus, Hiodon tergisus, Ictiobus bubalus, Carpiodes carpio, Cyprinus carpio, Ictalurus punctatus, Pomoxis annularis, P. sparoides,

Lepomis pallidus, Eupomotis gibbosus, Micropterus salmoides, and Perca flavescens.

For N. cylindratus two new host species are reported: Carpiodes carpio and Micropterus dolomieu.

Comparison with other Regional Studies

In his report on "Fish Entozoa from Yellowstone National Park" Linton (1893:555) listed but two species of Acanthocephala. They were given names of European species, though recent investigation has shown that extremely few species of fresh-water Acanthocephala are common to Europe and North America. Drawings and descriptions show that one species is of the genus Echinorhynchus and that the other is one of the Neoechinorhynchidae, though data are insufficient for the determination of species. This report by Linton constitutes as thorough a study of Acanthocephala as has been made for any fresh-water habitat in North America up to the present time; there is, consequently little data with which to compare the results of the present study; and, as indicated on an earlier page, there are few valuable European contributions with which comparison may be made.

Zschokke (1884) made an intensive study of the parasites from twelve of the most common species of fresh-water fishes from Lake Geneva, in Switzerland. In all, he examined over four hundred individuals, which yielded but three species of Acanthocephala; namely. Acanthocephalus lucii (= Echinorhynchus angustatus), Pomphorhynchus laevis (= E. proteus), and Neocchinorhynchus rutili (= E. clavacceps). Eight of the twelve species of fish studied were parasitized with Acanthocephala. In the locality examined by Zschokke the number of species of Acanthocephala is evidently very low when compared with the number of species found in the Illinois River. The genus Acanthocephalus, found in the European fishes, is wanting in the Illinois River fauna, while four genera of Neocchinorhynchidae occur in the Illinois River fish as against a single species revealed by Zschokke's study.

Lühe's check-list of parasites of European fresh-water hosts (1911) includes eight valid species of Acanthocephala characteristic of the fresh-water fishes of Europe. One additional species, *E. gadi*, is found in marine and migratory fishes, and is consequently taken into fresh-water habitats by the migratory fishes though not strictly characteristic of that habitat. Since Lühe in his list assembled the data concerning all known European fresh-water hosts, a comparison of his record with that for the Illinois River alone would be wholly inadequate; the writer has consequently included in Table II data for all fresh-water species of Acanthocephala known to belong to the North American fauna. The writer has previously (1915) discussed the difference in numbers of species of Acanthocephala infesting Amphibia on the two continents.

TABLE II

SPECIES OF ACANTHOCEPHALA REPRESENTED IN EUROPEAN AND NORTH AMERICAN FRESH-WATER HOSTS EXCLUSIVE OF BIRDS

PISCES

Genera of Acanthocephala	Species found in European hosts (Lűhe, 1911)	Species in Illinois River hosts	Species known to occur in North America
Echinorhynchus	salmonis clavula	thecatus	coregoni salvelini gadi (?)
Pomphorhynchus	laevis	bulbocolli	thecatus bulbocolli
Rhadinorhynchus Neoechinorhynchus	pristis	cylindratus	tenellus
TanaorhamphusOctospiniferGracilisentis		macilentus	crassus longirostris macilentus gracilisentis
	AMPHIB:	IA .	
Acanthocephalus	falcatus ranae anthuris		ranae
	REPTIL	IA	
Neoechinorhynchus	rutili (?)	emydis	emydis

Systematic Consideration of Species

So little has been written concerning the Acanthocephala of American fresh-water hosts that it seems desirable to bring together the scattered descriptions of the known species and to add to these the descriptions of a number of new species. This seems especially desirable in order that those interested in the study of economic problems, especially those connected with the fisheries industry, may have a ready means of identifying species in this important group of fish parasites. The older literature, even within its limited scope, does not meet this demand because of the failure of the earlier workers to recognize the distinctness of North American Acanthocephala from the Acanthocephala found on the Europeon continent. Again, many erroneous identifications of species have apparently extended the range of distribution for known forms owing to the inadequate available descriptions of the species reported upon. In the following section descriptions are given for the genera and species of Acantho-

cephala infesting fresh-water hosts of North America exclusive of the birds.

LINKINS' MANUSCRIPT SPECIES

In a manuscript thesis filed in the library of the University of Illinois, Mr. Ralph H. Linkins described two new species of Acanthocephala belonging to the genus Echinorhynchus. In the course of later study he described in manuscript another new species, belonging to the genus Pomphorhynchus. One of the species of Echinorhynchus, E. salvelini Linkins, was subsequently cited and described by Professor H. B. Ward (Ward and Whipple, 1918), under whose direction the thesis investigation was being conducted. Owing to his entering the Army, Mr. Linkins has been unable to put the results of his investigation into form for publication, and he has kindly granted the writer permission to quote from the manuscript descriptions in order that the species may be definitely cited in connection with the present work. The specific definitions of Echinorhynchus coregoni and Pomphorhynchus bulbocolli are entirely the result of work done by Mr. Linkins, to whom the writer wishes to give full credit.

Family ECHINORHYNCHIDAE

The family Echinorhynchidae was created by Hamann (1892) to include all of the Acanthocephala not set off in his other two families. Gigantorhynchidae and Neoechinorhynchidae. The species included in this heterogeneous group were, until a few years ago, all embraced in the one genus Echinorhynchus. Comparatively recent work, dating from the studies of Monticelli and of Lühe, has resulted in the erection of numerous genera from the disrupted genus Echinorhynchus. All of these genera, with the exception of those included in the Centrorhynchidae, are still retained in the family Echinorhynchidae. More thorough study of this unnatural assemblage of genera will probably lead either to the establishing of several families or, at least, to the recognition of subfamily groups within it. As the family now stands, little would be gained by an attempt to describe it, for there are very few characters common to all of the genera. Four genera usually assigned to this family are represented in the fresh-water fauna of North America. Each of these genera with its included species will be treated separately.

Echinoriiynciius Zoega, 1776

Generic Diagnosis.—Acanthocephala of small to medium size, parasitic as adults in the alimentary canal of fish. Subcuticula and lemnisci provided with numerous small nuclei or with a few very large finely dendritic nuclei. Body proper and neck spineless. Proboscis long, approximately cylindrical, armed with circles of hooks which are alternate in arrangement. Hooks of practically uniform size except those of a few basal circles, which are much reduced. Proboscis receptacle composed of

two layers of muscle inserted at the base of the proboscis. Central nervous-system near the middle of the proboscis receptacle.

ECHINORHYNCHUS THECATUS Linton, 1891

(Pl. XXII, Fig. 1-4)

Length: females, 11 to 26 mm.; males, 7 to 12 mm. In fully extended individuals both ends of the body are bent toward the ventral surface. Proboscis, when fully extended, frequently takes a position perpendicular to the axis of the body; in case of extreme extrusion may form acute angle with main axis of body. Proboscis usually about 1 mm. long. Neck about one-fourth the length of proboscis. Proboscis receptacle long and slender, about 1.5 times the length of proboscis. Central nervous-system located near the center of the proboscis-receptacle. Hooks alternate in arrangement; restricted entirely to proboscis; arranged in twelve longitudinal rows of twelve to thirteen hooks each. Lemnisci long and slender, about 1.5 times the length of proboscis-receptacle. Embryos within bodycavity of gravid female 80 to 110 μ long by 24 to 30 μ wide. The hooks at the base of the proboscis are 41 to 53 μ long, nearly straight, and in many instances each hook is completely ensheathed in a cuticular collar (Fig. 2). Near the middle of the proboscis, hooks of a much heavier form occur. These are rather uniformly about 71 µ long, although those on the ventral surface of the proboscis are more strongly curved and a little heavier than those on the dorsal (Fig. 2, 4). Hooks near the anterior tip are not so much recurved and not so strong as those near the middle though they reach greater length; namely, 77 to 89 μ. In the male eight cement glands are closely compacted at the posterior border of the hind testis.

Graybill (1902:197) has given a very good description of this

species, from which the foregoing data vary but slightly.

Hosts: Morone americana, Roccus americanus, Micropterus dolomieu, M. salmoides, Ambloplites rupestris, Amia calva, Lepisosteus platostomus, Hiodon tergisus, Ictiobus bubalus, Carpiodes carpio, Cyprinus carpio, Ictalurus punctatus, Pomoxis annularis, P. sparoides, Lepomis pallidus, Eupomotis gibbosus, Perca flavescens.

ECHINORHYNCHUS SALVELINI Linkins, 1918 (in Ward and Whipple)

(Pl. XXIII, XXIV, Fig. 5, 10, 12)

Body slightly enlarged anteriorly. Males 7 to 9 mm. long; 0.82 to 1.27 mm. in maximum diameter. Females 10 to 17 mm. long; 1.2 to 1.6 mm. in maximum diameter. Proboscis cylindrical, armed with 16 long: tudinal rows of about 13 hooks each. Basal hooks 39 to 50 μ long. Hooks on middle and anterior proboscis-regions 44 to 68 μ long, with basal process 83 μ long. Embryos 115 to 165 μ long by 20 to 25 μ broad; middle

shell of embryos forming polar prolongations which are more than twice as long as they are wide.

Host, Cristivomer nomayoush (Walbaum), the great lake trout.

ECHINORHYNCHUS COREGONI Linkins, n. sp.

(Pl. XXIII, XXIV, Fig. 6, 11, 13)

"Body enlarged at anterior end. Males 3 to 3.7 mm. long, maximum width 0.8 to 1.05 mm., at anterior one-fourth of body. Females 3 to 5.5 mm. long; widest part of body 0.6 to 1.5 mm. Proboscis cylindrical, carrying twenty circular rows of hooks, each circle containing six hooks. Hooks of adjacent rows alternate. Basal hooks 28 to 53 μ in length. Hooks in middle region of proboscis 65 to 80 μ in length. Terminal hooks smaller than those of middle rows. Ventral hooks larger and stronger than dorsal hooks. Embryos vary from 51 to 91 μ in length and from 17 to 20 μ in width. The common size is 77 by 19 μ ."

As indicated in an earlier part of this paper the above description is

quoted directly from a manuscript thesis by Linkins.

Host, Coregonus clupciformis.

Pomphorhynchus Monticelli, 1905; emended by Porta, 1907

Monticelli (1905:11) named the genus Pomphorhynchus in a footnote, without citing for it any type or characteristic species. Furthermore, he did not, in his definition, differentiate the genus, as later enended by Porta, (1907), from the genus Filicollis. Porta (1907:413) assigned Echinorhynchus proteus to the genus Pomphorhynchus, and since P. proteus is a synonym of P. locvis, the latter becomes the type of the genus.

There are numerous early records of the occurrence of "E. proteus" in North American fishes, but without much question they are all based upon misidentification of the species. The writer has examined numerous specimens from American hosts and has never found one which agreed with the detailed descriptions of the European species. All the examples of this genus that have come to the attention of the writer clearly belong to a new species, to which the manuscript name Pomphorhynchus bulbocolli has been assigned by Linkins. Linkins' description follows the generic diagnosis.

Generic Diagnosis.—Acanthocephala parasitic as adults in the alimentary canal of fish. Body unarmed. Neck very long, cylindrical except at its anterior extremity, where it expands into an approximately spherical bulla. The proboscis extends as an approximately cylindrical structure from the anterior region of this neck-enlargement. Tip of proboscis somewhat reduced in size. Proboscis receptacle inserted at the base of the proboscis, extending posteriorly through the neck, as a double-walled sac, into the anterior portion of the body-cavity proper. Central nervous-system at the posterior end of the proboscis-receptacle.

Pomphorhynchus bulbocolli Linkins, n. sp.

(Pl. XXIII, Fig. 7, 8)

Body clongate, tapering toward the posterior end. Neck prominent, measuring 2.6 to 4 mm. in length; diameter 0.15 to 0.4 mm. in posterior portion and 0.8 to 1.5 mm. in region of spherical enlargement. Proboscis cylindrical, 0.5 to 0.6 mm. long by 0.07 to 0.2 mm. wide; armed with twenty-four to twenty-eight circular rows of hooks. Basal circle with twelve hooks; remaining circles with six hooks each; hooks in circles anterior to basal circle alternating. Smallest hooks at tip of proboscis, about 16 μ long, with a diameter of 4 μ . Largest hooks, in seventh or eighth circle from tip, 36 to 40 μ long with a diameter of 22 μ . Hooks posterior to the eighth row 20 to 36 μ long with a diameter of 4 to 8 μ . Roots on hooks of first eight circles back from tip of proboscis 10 to 40 μ long. Embryos within body-cavity of gravid females 53 to 83 μ long by 8 to 13 μ in diameter; commonest size 63 by 10 μ .

Hosts: Ictiobus urus, I. bubalus, Carpiodes carpio, Cyprinus carpio, Ameiurus nebulosus, A. melas, Pomoxis annularis, and P. sparoides.

Intestine infested.

RHADINORHYNCHUS Lühe, 1911

Generic Diagnosis.—Acanthocephala parasitic as adults in the intestine of fish. Anterior body-region armed with scattered cuticular spines, ensheathed by cuticular folds. Proboscis and proboscis receptacle very long. Ventral proboscis-hooks stronger than dorsal. Proboscis receptacle a two-walled muscular sac with the brain located near its middle. Lemnisci long, finger-like.

This genus is not strongly represented in American hosts either from the point of view of species or of numbers of individuals encountered in the examination of fishes. It is typically a marine genus which is probably

occasionally brought into fresh-water by migratory fishes.

RHADINORHYNCHUS ORNATUS Van Cleave, 1918

Proboscis armed with from twenty-two to twenty-four longitudinal rows of about forty hooks each. Hooks on proboscis 50 to 80 μ long. Anterior body-region armed with scattered cuticular spines about 80 μ long. Embryos about 60 μ long.

Hosts, marine and migratory fishes.

Rhadinorhynchus tenuicornis Van Cleave, 1918

(Pl. XXIII, Fig. 9)

Proboscis armed with ten to fourteen longitudinal rows of approximately twenty-six hooks each. Proboscis hooks of female 40 to 80 μ long; those of male, near base, may be as short as 20 μ . Conspicuous crescent of about seven long spines on the ventral surface of the proboscis-

region at the division between neck and proboscis. Body spines of female 60 to 80 μ in length; those of male about 28 μ . Embryos within bodycavity of gravid females 60 to 80 μ long and 12 μ in diameter, with middle membrane drawn out into attenuated polar capsules.

Hosts: marine fishes, and "trout" from Baltimore—uncertain as to

whether marine or fresh-water trout.

ACANTHOCEPHALUS Koelreuter, 1771

Generic Diagnosis.—Acanthocephala of small to medium size, parasitic as adults in the alimentary canal of fishes and amphibians. Subcuticula and lemnisci provided with numerous small nuclei. Proboscis ovate or a short cylinder. Body proper and neck spineless. Proboscis receptacle a two-walled muscular sac inserted at the junction of proboscis and neck. Central nervous-system located at posterior extremity of proboscis-receptacle.

A single instance of the occurrence of specimens belonging to this genus is on record (Van Cleave, 1915) for the American continent. The specimens examined, agree in all essential details with the European

A. ranae, and have been identified as such by the writer.

ACANTHOCEPHALUS RANAE (Schrank, 1788)

Proboscis short, slightly larger in the middle than at extremities; armed with twelve to twenty longitudinal rows of four to seven hooks each. Largest hooks, near the middle of the proboscis, Ω to 80 μ long; hooks at anterior tip of proboscis about 60 μ long; those in basal row 30 to 50 μ . Embryos within body-cavity of gravid female about 110 μ long by 13 μ in diameter.

Host, Diemyctylus viridescens Raf.; Franklin Falls, Baltimore.

Maryland.

Family NEOECHINORHYNCHIDAE

DISTRIBUTION AND DIVERSIFICATION OF SPECIES

The Neoechinorhynchidae occur as adults chiefly in the intestine of fishes, though one North American species is restricted to the intestine of turtles. Hitherto only seven species have been considered as validly placed in this family. Of these, two occur in European hosts, while five, according to present records, are confined to the American continent. Recently, in examining the collections of Dr. G. R. La Rue taken from Douglas Lake, Michigan, the writer discovered an abundance of well-preserved material representing two new species of Neoechinorhynchidae, one of which clearly belongs to a new genus. Thus, with seven North American species, the family seems to have attained a much higher degree of differentiation on this continent than it has in Europe. This is evidenced not only by the greater number of species in the less thoroughly studied

American hosts, but even more strikingly in the greater diversification of

structure among the American species.

Hamann's description of the Neoechinorhynchidae (1892), based upon a knowledge of but one genus comprising two species of monotonous similarity, quite naturally emphasized for the family those characters which had been selected to characterize his Neorhynchus. The discovery of more strikingly diversified American species led the present writer (1913) to emend the generic diagnosis in order that N. gracilisentis and N. longirostris might be included within the genus Neoechinorhynchus (= Neorhynchus). However, more recent study has shown that the differences between these two species and the other members of the genus are too great to be regarded as of merely specific value. In the description of N. longirostris (Van C.) the writer (1913:182) pointed out the possibility of establishing a new genus for this species, but because of a few fundamental points of similarity in body-structure between this and other members of the family it was placed in the genus Neoechinorhynchus. Recent further study of Neoechinorhynchidae, made possible by the addition of newly discovered species, and a re-study of cotypes of N. longirostris have convinced the writer that the arguments originally advanced for retaining this species within the genus apply more strictly as reasons for its retention within the family. The validity of this position was seen by Professor Henry B. Ward who (1918:547) erected for it a new genus, Tanaorhamphus, with N. longirostris (Van C.) as type.

Inasmuch as the species *N. gracilisentis* (Van C.) possesses characters which give strong evidence of its generic isolation it becomes advisable to create for it a new genus, for which the writer proposes the name Gracilisentis, *Neocchinorhynchus gracilisentis* becoming the type of the

cenns

With the accumulation of new information and new interpretations of facts regarding members of this family more definite consideration should be given to the characterization of the family and of its constituent genera. In the following synopsis the writer has endeavored to describe the family and its genera in a more complete manner than has been attempted heretofore.

Family Characters

Acanthocephala of small to medium size, parasitic as adults in the alimentary canal of fishes and reptiles. Wall of proboscis-receptacle. Brain near base of proboscis-receptacle. Body devoid of spines; spines or hooks on proboscis only. Nuclei of subcuticula and of lemnisci extremely large, normally of fixed number and definite arrangement; the subcuticula with five in mid-dorsal line of body and one in mid-ventral line near anterior end; the lemnisci normally with two in one lemniscus and a single nucleus in the other. Embryos borne inside body of females provided with three membranes. Membranes in all known species fully concentric, without polar modifications or constric-

tions. Testes elliptical, usually contiguous. Cement gland a single syn-

cytial mass containing relatively few giant nuclei.

The giant nuclei furnish the most easily available characters for the recognition of members of this family. Subcuticular nuclei in members of the other families of Acanthocephala show a considerable degree of variability in size and in form, but in no case do they approach the condition found in this family. The dendritic nuclei of Echinorhynchus thecatus Linton are relatively difficult to demonstrate. In addition they differ so broadly from the form of the giant nuclei of the Neoechinorhynchidae that no confusion of the two is possible. The subcuticular nuclei are especially conspicuous in the Neoechinorhynchidae. Their location is clearly discernible as pronounced elevations of the body-surface both in living individuals and in preserved specimens even before staining. The number found in the subcuticula so far has been absolutely constant for every individual of the family examined, but their relative position within the dorsal and ventral lines of the body is subject to slight individual variability even within the confines of a given species. For example, the single nucleus of the mid-ventral line does not always bear a fixed relationship to the nuclei of the mid-dorsal line, but may be directly opposite the second dorsal nucleus or slightly anterior or posterior to it. The ratio of the spacing between the dorsal nuclei and the body-length is apparently an inconstant one.

The giant nuclei of the lemnisci are apparently constant both in number and in arrangement for all members of the family. In the examination of several hundred individuals, representing all the different genera, in every instance where conditions permitted close observation one lemniscus showed two giant nuclei while the other bore but a single one.

The cement gland of Neoechinorhynchidae shows considerable variation in the number of giant nuclei even within the confines of a single genus; but within species limits the number of nuclei in this gland is absolutely fixed. Bieler has found eight in the cement gland of N. agilis and twelve in that of N. rutili. As to Amercian species of Neoechinorhynchus, the writer has found eight giant nuclei in the cement gland of N. cylindratus, of N. cmydis, of N. tenellus, and of N. crussus. In Tanaorhamphus longirostris there are sixteen giant nuclei in the cement gland, while in Gracilisentis and in Octospinifer there are only eight.

The shape of the proboscis and the shape and number of the proboscis-hooks and their roots afford the most readily available charac-

ters for the separation of the genera of this family.

Synopsis of North American Genera and Species

NEOECHINORHYNCHUS Stiles and Hassall, 1905, sens. str.

Neorhynchus Hamann, 1892, preoccupied.

Eorhynchus Van Cleave, 1914.

Echinorhynchus Zoega, 1776, in part.

Generic Diagnosis.—Neoechinorhynchidae with short, globose proboscis armed with three circles of six hooks each. Terminal hooks conspicuously larger and heavier than those of remaining rows, and the only ones which bear conspicuous reflexed root-processes. Each root a broad, flattened disc, pyriform in surface view, usually approximately parallel to surface of proboscis wall. The thorn or hook proper attached at the apical or anterior end of the root, and appreciably longer than the root.

Of this genus three previously described and one new species are

found in North American hosts.

NEOECHINORHYNCHUS CYLINDRATUS (Van Cleave, 1913) (Pl. XXIV, XXV, Fig. 15, 17, 18)

Bodies large, almost cylindrical except in young forms, in which the posterior part is gradually narrowed. Females 10 to 15 mm. long, with a maximum diameter of 0.7 mm. a short distance back of the proboscis. Males 4.5 to 8.5 mm. long, with a diameter of 0.5 to 0.7 mm. Proboscis slightly broader than long (0.172 by 0.150 mm.). Hooks of terminal circle 79 to 97 μ long, 14 μ thick at base, each bearing a root 58 μ long and 29 μ broad. Hooks of middle row 37 μ long and 5 μ through at base. Basal hooks 21 to 25 μ long and 3 μ through at base. Embryos inside body of gravid female 49 to 51 μ long and 15 to 21 μ broad.

Type host, Micropterus salmoides; type locality, Pelican Lake,

Minnesota.

Additional hosts: Anguilla chrysypa, Micropterus dolomieu, Carpiodes carpio.

NEOECHINORHYNCHUS TENELLUS (Van Cleave, 1913) (Pl. XXIV, XXV, Fig. 16, 19, 20)

Bodies small, attenuated. Females 3.5 to 13 mm. long; 0.6 mm. in maximum diameter. Males 2 to 8 mm. long. Proboscis nearly cylindrical, 0.15 mm. long by 0.135 mm. wide. Hooks of anterior circle 90 to 110 μ long; those of middle circle 38 μ ; those of basal circle about 27 μ . Embryos 37 to 45 μ long by 12 to 16 μ broad.

Hosts: Esox lucius, Stizostedion vitrcum.

NEOECHINORHYNCHUS EMYDIS (Leidy, 1852) (Pl. XXIV, XXV, Fig. 14, 21, 22, 23)

Parasitic as adults in a limentary canal of turtles. Body much elongated, approximately cylindrical. Females 10 to 32 mm. long with average width of 0.7 mm. Males about 8 to 11 mm. long by 0.7 mm. wide. Proboscis globular, length usually equaling breadth; average length 0.18 mm. Terminal hooks 95 to 103 μ long, points usually reaching beyond bases of hooks of middle circle. Hooks of middle circle 49 to 59 μ long; those of basal circle 35 to 54 μ . Embryos within body cavity of gravid female oval, 16 by 11 μ .

Hosts: Graptemys geographica, G. pseudogeographica, Clemmys insculpta, C. guttata, "Emys serrata," Pseudemys elegans, P. troostii, P.

scripta, P. concinna.

NEOECHINORHYNCHUS CRASSUS, n. sp.

(Pl. XXVI, Fig. 24, 25, 28)

Body short and thick, almost cylindrical, tapering but slightly toward either extremity. Observed males 4 to 7 mm. long; females 6 to 9 mm. Maximum diameter of body usually in region of second dorsal subcuticular nucleus, just behind the single mid-ventral nucleus; in males usually slightly more than one-tenth of the total body-length, in females slightly less than one-tenth of the same. Body wall, especially the subcuticula, very thick, usually from 80 to 100 μ except in certain regions in anterior part of body of gravid females, where it becomes considerably thinner, frequently reaching only about 60 \(\mu\). Proboscis 0.27 to 0.325 nm. long and 0.24 to 0.27 mm. in diameter. Armed with three circles of six hooks each. Hooks of terminal circle only provided with prominent roots. Terminal hooks 94 to 100 μ long; hooks of middle circle 71 to 83 μ ; those of basal circle 47 to 71 μ. Proboscis receptacle typical of the genus in shape and structure; 0.45 to 0.6 mm. in length. Testes in largest males approximately the same size, 0.87 by 0.38 mm.; in broad contact with each other. In smaller males the anterior testis is the larger. Cement gland, in structure, typical of that described for the family; crowded into hind margin of posterior testis; approximately the same size as posterior testis except in largest specimens, in which it reaches 1,25 by 0.4 mm.; contains eight giant nuclei. Hard-shelled embryos within body of gravid female 35 by 14 μ .

Cotypes in collection of U. S. National Museum and in collections

of G. R. La Rue and of H. J. Van Cleave.

Host, Catostomus commersonii (Lacép.). Type locality, Douglas Lake, Michigan.

This species in many respects resembles the greatly variable Mediterranean species, N. agilis. The two species are, however, easily separated on the basis of general appearance even though the measurements and data usually given in specific definitions do closely agree. Biological evidence and morphological data taken together, give sufficient grounds for the ready differentiation of the two species. There is fairly strong evidence that N. agilis does not occur outside the Mediterranean, where it is found in fishes of the genus Mugil. Though fishes of this genus occur on the Atlantic coast of North America they have never been found to harbor any Acanthocephala. It seems improbable that a given species of Acanthocephala, N. agilis, for example, could have been brought to this continent by a marine fish and become established in an inland lake, leaving no trace of its transition from a marine to a fresh-water form. Numerous minor differences in structure give sufficient evidence of the distinctness of the two species even though ranges of variability in measurements for the two species frequently overlap. In general body-shape N. crassus is nearly cylindrical with a sudden diminution in size at each extremity, while N. agilis shows a conspicuous gradual tapering in both directions from the region of maximum diameter. The posterior two thirds of the body of N. agilis tapers, while only the tip of the body of

N. crassus is conical.

The body of N. crassus is much more robust than that of N. agilis. This appearance is due primarily to the greater thickness of the bodywall in crassus. In the region of maximum diameter of the body the wall of N. crassus rarely measures less than 80 μ , and is frequently $100~\mu$ thick, while in N. agilis the body wall in the same region rarely reaches a thickness greater than $40~\mu$. This same difference may be expressed in the ratio between the thickness of the body-wall and the diameter of the body-cavity. In N. crassus the maximum diameter of the body-cavity is not more than eight times the thickness of the body-wall, while it is usually only about five times the thickness of the wall. In specimens of N. agilis studied by the writer the maximum diameter of the body-cavity is frequently eighteen or twenty times the thickness of the body-wall.

The proboscis of N. crassus is conspicuously larger than that of

N. agilis.

The male reproductive organs in N. agilis are usually located farther from the posterior tip of the body than in N. crassus, and therefore the ducts leading from the cement gland and from the testes are longer in the former than in the latter.

The cotypes upon which the description of *N. crassus* is based were collected by Dr. George R. La Rue from the intestine of the common

sucker, at Douglas Lake, Michigan, July 20, 1912.

Octospinifer, n. gen.

Generic Diagnosis.—Proboscis short, globose, usually slightly broader than long; provided with three circles of eight hooks each. Hooks of terminal circle not much larger or stronger than hooks of middle circle and but little longer than the root process. Testes elliptical, in contact with each other but not joined by a broad contact-surface. Cement gland not in direct contact with posterior testis. The two lemnisci dissimilar in nuclear content, one possessing two giant nuclei and the other a single one. Central nervous-system located at one side of the proboscis-receptacle, near its base.

Type species, Octospinifer macilentus.

Octospinifer macilentus, n. sp.

(Pl. XXVI, Fig. 26, 27, 29)

Body long, approximately cylindrical, tapering slightly toward posterior extremity. Males about 4 mm. long. Females about 10 mm. long; maximum diameter about 0.4 mm., although in some gravid females its as great as 0.58 mm. Genital opening of female on ventral surface about 0.1 mm. from the posterior extremity of the body. Posterior extremity of body about 0.19 mm. in diameter. Proboscis short, globular, usually slightly broader than long; length about 0.106 mm., diameter about 0.120 mm. The eight hooks of terminal circle equal in size; not conspicuously

larger than hooks of remaining circles. Terminal hooks 41 μ long; hooks of middle circle 32 to 35 μ ; those of basal circle 24 to 30 μ . Testes elliptical, not crowded together. Sperm ducts of mature males frequently showing a number of vesicular enlargements between the posterior margin of anterior testis and the anterior margin of the cement-glaind. Cement gland not in close contact with posterior testis, frequently broadly separated from it; form typical of the family, containing eight giant nuclei. Embryos within body-cavity of mature females 30 to 47 μ long by 15 to 18 μ wide.

Type host, Catostomus commersonii (Lacép.); type locality, Douglas

Lake, Michigan.

Cotypes deposited in the U. S. National Museum and in the collections of G. R. La Rue and of H. J. Van Cleave. The material from which this species was described was collected by Dr. George R. La Rue in July and August, 1912.

GRACILISENTIS, n. gen.

Neoechinorhynchus, in part; (= Neorhynchus = Eorhynchus).

Generic Diognosis.—Neoechinorhynchidae of small size, parasitic in the digestive tract of fishes. Body proper unarmed. Proboscis provided with three circles of twelve hooks each. Each thorn ensheathed in a prominent cuticular collar which permits only a small portion of the thorn to protrude from the surface of the proboscis. Each hook of the terminal circle provided with a conspicuous root-process several times longer than the exposed portion of the spine. Root composed of a broad flat basal area which, by gradual diminution in size anteriorly, makes an ill-defined transition from thorn to root. Basal region of terminal roots frequently slightly indented. Hooks of middle circle similar in general form to those of terminal circle except that root processes are shorter and less easily observed. Basal hooks without recurved roots.

Type species, Gracilisentis gracilisentis (Van Cleave, 1913).

Gracilisentis gracilisentis (Van Cleave, 1913)

(Pl. XXVII, Fig. 30, 31, 32)

Body small, tapering slightly at either extremity; extremities bent toward ventral surface, forming a slight crescent. Fully mature females 1.7 to 4 mm. long, greatest diameter slightly anterior to middle of body, 0.38 mm. Males 1.5 to 3 mm. long, greatest diameter 0.3 mm. Proboscis approximately pear-shaped, usually with a slight constriction between the middle and basal circles of hooks. All hooks very delicate; those of terminal circle 15 to 17 μ long, with a root 20 μ ; those of second circle 12 to 15 μ , with root about 15 μ long; those of basal circle almost straight, 15 to 20 μ long, without root. Cement gland containing eight giant nuclei. Embryos conspicuously spindle-shaped 36 to 40 μ long by 10 μ broad.

Type host, Dorosoma cepedianum (LeS.); type locality, Illinois River

at Hayana, Illinois.

TANAORHAMPHUS Ward, 1918

Neoechinorhynchus, in part; (= Neorhynchus = Eorhynchus).

Generic Diagnosis.—Neoechinorhynchidae of small to medium size, with cylindrical proboscis several times longer than wide. Proboscis armed with about sixteen longitudinal rows of hooks. Rows frequently incomplete and imperfect. Cement gland of type characteristic of the family.

Type species, Tanaorhamphus longirostris (Van Cleave, 1913).

Tanaorhamphus longirostris (Van Cleave, 1913)

(Pl. XXVII, Fig. 33, 34, 35)

Neoechinorhynchus longirostris (Van Cleave, 1913).

Body robust, with posterior extremity slightly flexed ventrad. Proboscis when fully extended inclined toward ventral surface at conspicuous angle. Females average about 6 mm. in length and have a diameter of about 0.63 mm. Males average 4 mm. in length and have a maximum diameter of 0.47 mm. Proboscis cylindrical, 0.5 mm. long, and with a diameter of 0.15 mm. Hooks rather irregularly arranged in about sixteen to twenty longitudinal rows with about ten hooks in each row. Largest hooks near anterior end of proboscis, about 54 μ long. A few hooks near the base of the proboscis about 16 μ long. Cement gland with sixteen giant nuclei. Embryos within body-cavity of gravid female 27 μ in length by 8 to 10 μ in diameter.

Type host, Dorosoma cepedianum (LeS.); type locality, Illinois River

at Havana, Illinois.

EUROPEAN SPECIES

REEXAMINATION OF THE TYPES OF N. agilis (Rudolphi)

European representatives of the genus Neoechinorhynchus have been characterized by European parasitologists in widely different descriptions. Attempting to use these definitions of species in studying members of the same genus from North American hosts, the present writer found the characterizations so diverse that it was difficult to determine whether the conflicting data represented individual variability within the species or resulted from inaccurate observations and erroneous identification. The records of each of a number of the investigators are so inconsistent that tabulated comparisons of the data when considered alone afford practically no key to the solution of the problems of specific identity. Fortunately, through the efforts of Professor Henry B. Ward, the writer, in 1913, had the rare good fortune to secure from the Berlin Museum, for examination, two "type" specimens of N. agilis (Rudolphi). A comparison of these with the descriptions of European investigators and with other specimens from European hosts constitutes the basis of the discussion which follows.

Rudolphi's description of N. agilis (= Echinorhynchus agilis) was based upon an examination of nine individuals taken from the intestine of Mugil cephalus at Spezia. The above-mentioned alcoholics from the Berlin Museum (Catalog No. 1179) had in the vial with them a label indicating that they were "types" of Echinorhynchus agilis from the collection of Rudolphi. It is very apparent that the term type specimens was here used in the older meaning of the term, indicating a type-lot of material upon which a specific description was based, not referring to a single individual. In spite of the fact that these specimens had been preserved in alcohol for almost a century they were in good condition for examination. Because of the difficulties involved in the technic of dehydrating and clearing Acanthocephala, and because of the uncertainty of the success accompanying this procedure with such a limited number of unreplaceable specimens, the writer confined his examination to those observations which could be made upon the specimens while in alcohol.

Unfortunately, the individuals were both males, and consequently no facts regarding the embryos were available. The proboscis, fortunately, was extended fully in both specimens. The body of only one of the worms was perfect, the other lacking the posterior region of the body. In Table III the perfect individual is referred to as 1179A: the mutilated one, as 1179B. Careful observations were made upon the proboscis hooks of these specimens, but since the specimens were not cleared, measurements of books could be obtained for only those portions protruding beyond the proboscis-wall. As shown in the table, the two individuals differed considerably in the length of the exposed portions of the hooks (see also Pl. XXVIII, Fig. 42, 43). It is interesting to note that this type material furnishes the key to an understanding of the variability in hook-length found for different individuals of this species as brought out in a later part of this paper.

 $\label{table III}$ Data from Study of "Type" Material of $N.~agilis~(\mathrm{Rud.})$

	1	Prob	oscis	Length, exposed portion of hooks				
	Body-length	Length	Width	Terminal	Middle	Basal		
1179 A	3.3 mm.	160 μ	148 μ	49 μ	16 μ	11 μ		
1179 B	Incomplete	148 μ	153 μ	54 μ	21-27 μ	20 μ		

Comparison of N. agilis Data from Various Sources

Through the generous response of Professor Corrado Parona, of Genoa, and of Professor Fr. Sav. Monticelli, of Naples, the writer was supplied with collections for comparison with the "type" specimens 1179A and 1179B. The close resemblance between alcoholic specimens received

from these two investigators and the two "types" in question left no room for doubt of their specific identity. The writer has since made careful study of stained whole-mounts and of serial sections with a view towards a more exact determination of the characters of the species as defined by Rudolphi.

Specimens received from Professor Monticelli collected at Trieste by Stossich from Mugil sp?, possess hooks of uniformly smaller average size (Pl. XXVIII, Fig. 38, 39) than those collected by Professor Parona from Mugil awatus and M. cephalus at Genoa. The differences are not, however, great; nor are they discontinuous (Fig. 36, 37). In all instances the ranges in size of the various hooks for the two collections overlap. This may indicate a slight tendency within this species toward the differentiation of geographical varieties. Varieties have not, however, become definitely enough fixed to warrant an attempt to separate them. In the light of this evidence of divergence it seemed worth while to investigate typical instances of measurements ascribed to members of this species by various writers. Table IV presents data for this comparison.

Table IV $\label{eq:definition} \text{Data from Descriptions of N. $agilis$}$ (Measurements are in \$\mu\$)

Observers	Date	Locality	Number of circles of hooks	Number of hooks in each circle	Length of terminal hooks	Length of middle hooks	Length of basal hooks	Proboscis length	Proboscis diameter	Length of embryos	Diameter of em- bryos	Number of testes
Dujardin,	1845	Toulouse and Rennes		6	110	74	65	140		43	14	3
Stossich	1885	Trieste ?	3-4	6?								3
Hamann	1895	?	3	6	150	70	[70?]	,		26		2
Condorelli	1898	Rome	3	6	131	85	65	334	250	36	15	
Porta,	1905	?	3-4	6:	70	50	20	200-300	100-200	26		
Van Cleave (Monticelli Coll.)	1919	Trieste	3	6	94-106	41-82	30-65	150-250	185-230	30-41	12-15	2
Van Cleave(Parona Coll.)	1919	Genoa	3	6	94-120	65-83	41-71	180-270	150-200	30-41	12-15	2

The cement gland in this species has been very generally misinterpreted. Dujardin, in describing three testes, obviously mistook the cement gland for a testis. Stossich made the same error. Hamann reported six cement glands, though in fact only a single large syncytial

mass is present. Bieler has called attention to the fact that this peculiar type of cement gland is distinctive for the family Neoechinorhynchidae and has discovered that eight giant nuclei are always present in the cement gland of N. agilis. The last statement has been corroborated by

the observations of the present writer.

Stossich was in error in regard to the number of circles of hooks upon the proboscis. It seems probable that this error resulted from his basing his description upon the study of a poorly executed drawing (see Fig. 41, Pl. XXVIII) in which the hooks of the terminal circle were so grossly distorted that they have the appearance of belonging to two entirely distinct circles. Notwithstanding the fact that Porta (1905:213) in the explanation of his plate indicates that Figure 12 of N. agilis is original, it bears a striking likeness (see Fig. 40, Pl. XXVIII) to the figure given by Stossich (1885). The peculiar misrepresentation of the hooks and of their arrangement is identically the same in the two figures. The two hooks of the terminal circles seen in profile appear to be of an entirely different order from the remaining hooks of that circle, which are much distorted through foreshortening. As a consequence of this error in observation Porta (1905:166) was induced to consider Echinorhynchus hexacanthus Dujardin as a synonym of N. agilis, believing the species to be greatly variable not only in regard to the dimensions of the hooks, but with reference to the number of hooks as well. In spite of this belief, his own description of N. agilis ignores the extent of this variability and includes but a single measurement for each type of hooks.

The present writer, after examining hundreds of specimens belonging to four different species of Neoechinorhynchus, has failed to find a single individual deviating from the typical arrangement of three circles bearing six hooks each. In Porta's description his "armata di 15-18 uncini disposti in 3-4 serie.", implies a variation which would necessitate a revision of the original description of the species, since even as early a worker as Rudolphi included in his description of the species a statement of the constant relations of these hooks. Porta's statement, involving a radical departure from the observations of other workers in the field,

must inevitably be regarded as problematical in the highest degree.

VARIABILITY IN N. agilis

As shown in Table IV. Hamann has given a measurement for the terminal hooks of N. agilis more than twice that given by Porta, yet neither writer has given any attention to the range of variability in the size of the hooks. It is not impossible that Porta considered only the protruding portions rather than the entire hooks, but even on this assumption his descriptions and his drawings can not be made to agree. According to his text, hooks of the basal circle are less than half the length of those in the middle circle; yet his figure shows practically no difference in the lengths of these two types of hooks.

In considering the range of variability of the proboscis hooks for any species of Acanthocephala the mechanical difficulties involved in obtaining exact measurements of these structures must be duly regarded. Exact measurements are possible only in cases where the hooks are viewed in full profile; accordingly, in a permanent mount usually not more than one or two hooks of any given circle will afford conditions for obtaining an accurate determination of the maximum length of the hooks. For all other hooks there is usually a foreshortening produced by the angle at which the hooks protrude toward the observer from the proboscis-wall. In order to determine the extent to which variability in hook-length may go in N. agilis, the writer has taken numerous measurements in which especial care was exercised to eliminate inexact and incorrect observations. In Table V are brought together a few typical examples of measurements which were obtained from a study of individuals from the collections of Parona and of Monticelli.

TABLE V
VARIABILITY OF HOOK-LENGTH IN N. agilis
(Measurements are in μ)

Slide No.	Sex	Terminal hooks, length	Middle hooks, length	Basal hooks, length
Parona Coll.	1		1	
618	Ω	94	*	41-47
619	♀ ⋄ ⋄ ♀	120	71	59
620	P	120	71	59-65
622	3	120	77	71
623	8 8	120	65	65
624	3	120	83	59-71
Monticelli Coll.				
714	8	94-100	53	35
715	8	100	53	30
716	8	94-100	41-47	30-35
717	Q	tips broken	47	35
718	\$0 \$0 \$0 O+ O+ \$0 \$0	tips broken	47-53	35
719	8	106	71-82	53-65
720	8	106	65-71	47

^{*} No hook in a position for an accurate measurement.

Because of the differences in data concerning N. agilis presented by various workers, only a part of which seem explicable on the ground of individual variability within the species, it seems desirable that a full statement be given covering the diagnostic characteristics of this species. The following description is based upon the comparison of recent European collections with Rudolphi's types of the species. In the case of varying structures an attempt has been made to indicate the usual range of such variability.

Neoechinorhynchus agilis (Rudolphi, 1819) (Pl. XXVIII, Fig. 36-44)

Specific Diagnosis.—Maximum diameter in anterior third or fourth of body. From this region body tapers gradually toward each extremity.

Proboscis usually slightly longer than wide, provided with three circles of six hooks each. Hooks of terminal circle provided with a conspicuous reflexed root-process approximately one-half the length of the hook proper. Terminal hooks 94 to 120 μ long. Middle circle composed of hooks 41 to 83 μ long, with one short basal process extending anteriorly and another posteriorly from the point of origin of the hook proper. Basal hooks 30 to 71 μ long with no conspicuous root, frequently with a small process similar to the one described for the hooks of the middle circle. Embryos within the body of gravid female approximately elliptical, 26 to 41 μ long by 12 to 15 μ in diameter. Testes two, approximately elliptical, in broad contact with each other; followed posteriorly by a syncytial cement-gland containing eight giant nuclei.

Type host, Mugil cephalus; intestine infested.

Type locality, Spezia, Italy.

Distribution.—The writer has already (1913:188) called attention to the fact that records by Linton of the occurrence of this species in North American fish are based upon misidentifications. It is interesting to note that while Mugil cephalus and other species of the same genus occur along the Atlantic coast of North America, no Acanthocephala have been reported from any of them in Linton's extensive records of the

examinations of marine fish for parasites.

The reports of *N. agilis* from Scotland by Thomas Scott and from France by Dujardin are the only other reports known to the writer of the supposed occurrence of this parasite outside the Mediterranean region. Of these, Scott's identification is not at all certain. General appearance of the parasite and the species of the host were the only two points which caused him to place his specimens under this name. His figures are clearly enough of a species of Neoechinorhynchus, although they are not distinctive or definite enough to justify the assumption that they represent *N. agilits*.

It seems probable that N, agilis is restricted in its distribution to the

fishes of the genus Mugil in the Mediterranean region.

Neoechinorhynchus rutili (Müller, 1780)

Of the fresh-water representative of this genus in Europe, the writer has not been able to secure specimens for study. European investigators seem inclined to agree with Lühe in regarding $Echinorhynchus\ clavacceps$ as a synonym of $N.\ rutill$. This last species thereby becomes the only valid species of the genus reported from fresh-water fishes of central Europe. This claim of synonymity is obviously based upon a literature study rather than upon examination of type specimens of the species concerned. Much of the work of European investigators has unfortunately been of this character. It is certain that none of the early descriptions, dating back more than a century, include data which, alone, would suffice to differentiate species of the family Neoechinorhynchidae. The following table indicates typical discrepancies in the data recorded for $N.\ rutill$ (= $E.\ clavacceps$).

Table VI

Data from Descriptions of N. rutili and E. clavacceps

(Measurements are in μ)

			Len				
Author	Date	Species	Terminal	Middle	Basal	Embryos	
Lühe Hamann Porta Dujardin	1911 1891 1905 1845	rutili clavaeceps clavaeceps clavaeceps	170 70 70 67	100 30 30 44	[100?] [30?] [30?] 41	38 by 19–21 41 35 by 17 41	

The fresh-water representatives of this genus in Europe truly need the attention of some careful worker to ascertain if all belong to the same species. If Lühe's synonymy is correct some one should study the interesting case of variability in N. rutili since he reports specimens having terminal hooks 170 µ long, while Hamann found that typical individuals had hooks but 70 µ long. If one could have implicit faith in the data presented by these authors there would be ample ground for the recognition of two distinct species; but their descriptions are too inconsistent and contradictory to justify such a course. Hamann (1891, Pl. IX, Fig. 3) figures the terminal hooks of E. clavaeceps as less than 50 per cent. longer than the hooks of the middle circle, while in the same article he describes them as more than twice as long. Similarly, in Figure 17 of the same plate he shows the terminal hooks as only 25 per cent. longer than those of the middle circle. Lühe (1911, Fig. 2) obviously made an error in the calculation of the magnification of his drawing of the proboscis of N. rutili. On the basis of the stated magnification the terminal hooks are only $64 \mu \log$, instead of 170 μ as stated in the text.

Since N. rutili is regarded as the type of the genus, it is an unfortunate circumstance that there is so great lack of agreement in the available descriptions. If Porta, Dujardin, and Hannann are correct, the chief means of distinguishing this species from N. agilis lies in the smaller size of the terminal proboscis-hooks of the former, though Lühe would have us believe that the chief distinction lies in the larger terminal-hooks of rutili. Bieler has offered one means of separating N. agilis and N. rutili based upon the number of giant nuclei in the cement gland of the male, but he simply states that the former has eight giant nuclei while the latter has twelve. He has given no statement of other diagnostic features avail-

able for the separation or characterization of the species.

THE IDENTIFICATION OF SPECIES

The Acanthocephala present few characteristics available for ready identification of species. Through adaptation to the parasitic habit the body proper has become reduced to little more than an elongated sac

containing the reproductive organs. With few exceptions this sac presents the same external appearance in different species, though members of some genera are readily distinguishable by the presence of spines upon the body-covering. General body-shape and size differ with the age of the individuals, but certain features of body-form are of value in the recognition of species if used in connection with other characters of a more stable nature. In view of this fact, outline drawings of entire individuals of many of the species are presented, for the first time, in this paper.

Unfortunately, the proboscis, upon which much importance is placed in classification, is frequently completely invaginated within the body. Living specimens may be induced to protrude the proboscis if left for a few minutes in a dish of plain water, though they are best studied in

normal salt-solution.

Stained whole-mounts and sections are needed for the study of internal organs and for an accurate study of the proboscis hooks. Preliminary to the preparation of these, the worms should be placed for about fifteen minutes in a saturated solution of corrosive sublimate to which enough acetic acid has been added to make a one per cent. mixture. After washing in water the specimens should be passed through 35 and 50, to 70 per cent. alcohol in which they may be kept indefinitely. In the preparation of whole mounts and of sections ordinary histological procedure is followed. Best results are obtained if the body wall is pierced in a number of places with a fine needle. This prevents shrinkage when specimens are changed from one liquid to another. A very dilute mixture of Ehrlich's acid hematoxylin in distilled water has been found to be one of the most valuable stains for whole mounts in danar and for sections.

In the following key an attempt has been made to utilize characters which are easily observable even in living or in alcoholic specimens. In most instances, however, the separation of species involves careful study

of permanent mounts and of sections.

7 (8)	Proboscis bearing three circles of twelve hooks each
8 (7)	Proboscis bearing three circles of less than twelve hooks each
9(10)	Eight hooks in each circleOctospinifer macilentus, n. sp
10 (9)	Six hooks in each circle1
11(12)	Hooks of basal circle over 40 μ long. Body wall about 80 μ thick
	Neoechinorhynchus crassus, n. sp
12(11)	Hooks of basal circle less than 40 μ long
13(14)	Body very long, approximately cylindrical. Embryos within body of gravid female usually over 48 μ long Neoechinorhynchus cylindratus
14(13)	Body tapering conspicuously from anterior region toward the posterior extremity. Embryos within body of gravid female less than 45 µ long
15 (4)	Proboscis variable in shape but never globular; always bearing more than three circles of hooks
16(17)	Proboscis long, approximately cylindrical. Body of almost same diameter throughout. Cement gland a single syncytial mass. Proboscis receptacle a single walled sac. Giant nuclei of subcuticula plainly observable in stained specimens
17(16)	Proboscis long or approximately ovoid. Male bearing several separate and distinct cement-glands, variously grouped. Proboscis receptacle a double-walled sac. Nuclei of subcuticula small and numerous or finely dendritic
18(19)	Brain located at base of proboscis-receptacle. Retinacula coming off from posterior end of receptacle. In intestine of amphibian
19(18)	Brain located some distance anterior to the posterior end of proboscis- receptacle. Retinacula given off from sides of receptacle20
20(23)	Anterior region of body slightly inflated and larger than posterior portion, which tapers gradually toward posterior extremity21
21(22)	Proboscis bearing sixteen longitudinal rows of hooks. Embryos within body of gravid female 115 to 165 μ long, the middle membrane drawn out into polar prolongations more than twice as long as wide
22(21)	Proboscis bearing tweive longitudinal rows of hooks. Embryos within body of gravid female 51 to 91 μ long, the polar prolongations of middle membrane usually not much longer than wide
23(20)	Body tapering gradually from anterior region posteriorly. Lemnisci long. Embryos 80 to 110 μ long $Echinorhynchus$ thecatus.
24 (1)	Body proper provided with cuticular spines in anterior region. Proboscis long, cylindrical. Parasitic in intestine of fish25
25(26)	Proboscis armed with twenty-two to twenty-four longitudinal rows of hooks
26(25)	Proboscis armed with ten to fourteen longitudinal rows of hooks

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Explanation of Plates

All figures unless otherwise indicated are original and were drawn with a camera lucida. In closely related species all drawings of the same structures are drawn to the same scale, thus permitting direct comparison of figures.

SYMBOLS USED

- c, cuticular sheath surrounding proboscis hooks
- cg, cement gland
- g, ganglion of central nervous-system
- an, giant nucleus
- l, lemniscus
- n, neck
- p, polar prolongation of middle membrane of embryo
- r, receptacle of the proboscis
- t, testis

July, 1919.

PLATE XX11*

Echinorhynchus thecatus

Fig. 1. Optical section of immature male showing general form and arrangement of organs. Sexual organs in this individual not mature. From intestine of Micropterus salmoides. Stained with hematoxylin and mounted in damar.

Fig. 2. Profile of dorsal surface of proboscis, showing a single longitudinal row of hooks. Same individual as shown in Fig. 1.

Fig. 3. Embryo from body-cavity of mature female.

Fig. 4. Profile of proboscis, ventral surface, showing a single longitudinal row of hooks.

 $^{^{6}\}text{The scale}$ indicating magnification of Fig. 1 has a value of 1 mm.; that of Fig. 2 and 4, 0.1 mm.; that of Fig. 3, 0.05 mm.

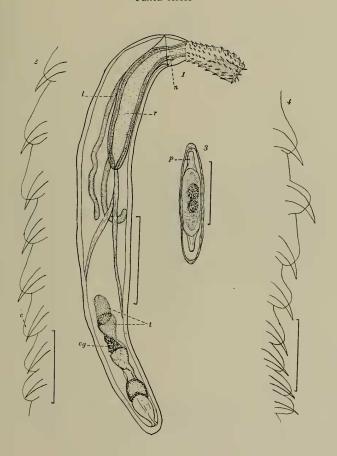


PLATE XXIII *

Fig. 5. Echinorhynchus salvelini. Embryo from body-cavity of gravid female, showing very long polar prolongations of middle membrane.

Fig. 6. Echinorhynchus coregoni. Embryo from body-cavity of gravid female, showing short polar prolongations of middle membrane.

Fig. 7. Pomphorhynchus bulbocolli. Optical vertical section of immature male taken from intestine of Ameturus nebulosus. Whole mount, stained with hematoxylin and mounted in damar.

Fig. 8. P. bulbocolli. Embryo from body-cavity of gravid female taken from intestine of Ictiobus urus.

Fig. 9. Rhadinorhynchus tenuicornis. (Van Cleave, 4918a.)

 $^{^{*}}$ Scales indicating magnification have a value of 0.05 mm. in all figures except Fig. 7, in which the scale-value is 1 mm.

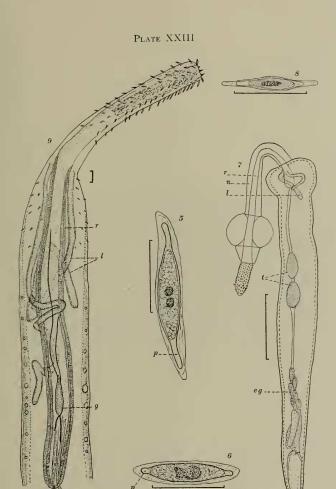


PLATE XXIV *

Fig. 10. $Echinorhynchus\ salvelini$. Profile of ventral margin of proboscis of fully mature female. Stained in hematoxylin and mounted in damar.

Fig. 11. Echinorhynchus coregoni. Profile of ventral margin of proboscis of fully mature female. Stained in hematoxylin and mounted in damar.

Fig. 12. E. salvelini. Outline showing general body-form of fully mature female. Body cavity is so packed with embryos that internal structures are completely obscured. Whole mount in damar.

Fig. 13. $E.\ coregoni$. Outline of fully mature female. Note contrast in body-form and size of this species and of $E.\ salvelini$.

Fig. 14. Neocchinorhynchus emydis. Surface view of proboscis of fully mature female from intestine of *Graptemys pseudogeographica*. Hematoxylinstained specimens in damar.

Fig. 15. $N.\ cylindratus$. Surface view of proboscis of fully mature female from $Micropterus\ salmoides$. Whole mount in damar.

Fig. 16. N. tenellus. Surface view of proboscis of fully mature female from Sticostedion vitreum. Stained in hematoxylin and mounted in damar. The hook shown in broken outline lies behind the median plane. Terminal hooks in this species point more directly backward than in other members of the genus.

^{*} Scales indicating magnification of Fig. 12 and 13 have a value of 1 mm.; all others in the plate have a value of $0.05\ mm$.

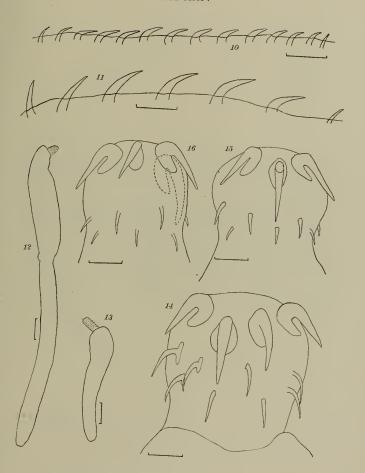


PLATE XXV *

Fig. 17. Neocchinorhynchus cylindratus. Outline showing general body-form and size of fully mature female from intestine of Micropterus salmoides. Positions of giant nuclei of subcuticula are indicated. Body completely filled with developing embryos, which obscure all internal structure. Hematoxylin-stained mount in damar.

Fig. 18. Embryo from body-cavity of female shown in Fig. 17.

Fig. 19. N. tenellus from intestine of Stizostedion vitreum. Outline of gravid female, showing general body-form. Hematoxylin-stained whole-mount in damar.

Fig. 20. Embryo from body-cavity of specimen shown in Fig. 19.

Fig. 21. Neoechinorhynchus emydis from intestine of Graptemys pseudo-geographica. Outline showing general body-form of gravid female with body-cavity completely packed with embryos.

Fig. 22. Optical section of immature male of same species. A comparison of this figure with the preceding one shows how slightly the increase in body size due to growth modifies the general body-form.

Fig. 23. Embryo from body-cavity of gravid female of same species.

^{*} Scales indicating magnification of Fig. 17, 19, and 21 have a value of 1 mm.; all others in the plate have a value of 0.05 mm.

PLATE XXV

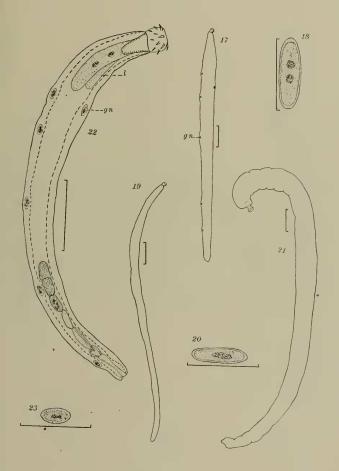


PLATE XXVI *

Fig. 24. Ncoechinorhynchus crassus, n. sp., from intestine of Catostomus commersonii. Optical section of mature male, showing arrangement of internal organs and relative thickness of body-wall. Hematoxylin-stained whole-mount in damar.

Fig. 25. Surface view of proboscis of same individual.

Fig. 26. Octospinifer macilentus, n. sp., from intestine of Catostomus commons on Drical section of mature male. From hematoxylin-stained whole-mount in damar.

Fig. 27. Surface view of proboscis of same individual.

Fig. 28. Neoechinorhynchus crassus. Embryo from body-cavity of gravid female.

Fig. 29. Octospiniter macilentus. Embryo from body-cavity of gravid female.

 $^{^{*}}$ Scales indicating magnification of Fig. 24–26 have a value of 1 mm.; all others in the plate have a value of 0.05 mm.

PLATE XXVI

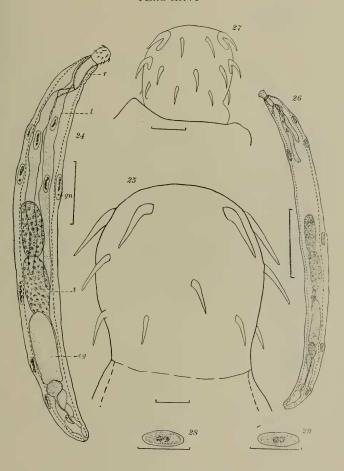


PLATE XXVII *

Fig. 30. Gracilisentis gracilisentis from intestine of Dorosoma cepedianum. Optical section of fully mature male. Whole mount in balsam, stained in hematoxylin.

Fig. 31. Surface view of proboscis of gravid female of same species, showing types of hooks and their arrangement. Paracarmine-stained whole-mount in balsam.

Fig. 32. Embryo from body cavity of gravid female of same species.

Fig. 33. Tanaorhamphus longirostris from intestine of Dorosoma cepedianum. Optical view of fully matured male. Hematoxylin-stained specimen in balsam.

Fig. 34. Embryo from body-cavity of gravid female of same species.

Fig. 35. Hooks from surface of proboscis of gravid female of same species, showing difference in size and form characteristic of different regions: (a) profile of eighth hook from base of proboscis in one of the longitudinal rows upon the ventral surface; (b) fifth hook from the base in a row upon the lateral surface of proboscis; (c) fourth hook from base of proboscis in a longitudinal row upon the ventral surface.

^{*} Scales indicating magnification of Fig. 30 and 33 have a value of 1 mm.; all others in the plate have a value of 0.05 mm.

PLATE XXVII

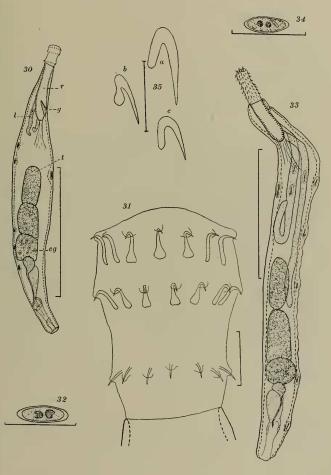


PLATE XXVIII *

Neoechinorhynchus agilis

(Fig. 36-39 illustrating variability in proboscis and in hook-length)

Fig. 36. Hooks from a long-hooked individual (male) from the collection of Parona: (a) hook from terminal circle; (b) hook from middle circle; (c) hook from basal circle,—all in full profile.

Fig. 37. Surface view of proboscis of a typical long-hooked individual from collection of Parona. In this figure and in Fig. 39 the hooks on the extreme back of the proboscis are omitted. Roots of hooks, shown in broken outline, lie behind the median vertical plane.

Fig. 38. Hooks from short-hooked individual (male) from the collection of Monticelli. Letters have same significance as in Fig 36.

Fig. 39. Prohoscis of a typical short-hooked individual from above collection. Fig. 40. Proboscis. (Copied from Porta—1905, Pl. I, Fig 12. Surface-shading omitted.)

Fig. 41. Proboscis. (Copied from Stossich—1885, Fig. 19.)

Fig. 42. Proboscis of 1179B—an alcoholic specimen from "type" material of Rudolphi.

Fig. 43. Proboscis of 1179A-alcoholic specimen from same material.

Fig. 44. Embryo from body-cavity of gravid female from collection of Monticelli.

 $^{^{\}rm s}$ Scale indicating magnification of Fig. 44 has a value of 0.01 mm.; all other scales in the plate have a value of 0.1 mm.

PLATE XXVIII

